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# Predator-pressure on earthworms: field experiments in a beechwood

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With 8 figures

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## 1. Introduction

At a study site in a calcareous beech forest near Göttingen (FRG), there has been a long-term program of ecosystem analysis (SCHAEFER, 1982 & 1989). In the descriptive part of the studies earthworm populations displayed a considerable amount of seasonal and between-year fluctuations (JUDAS *et al.*, 1989). As in any ecological system the question arises, which biotic and abiotic factors determine population dynamics to what degree. In this paper experiments on the influence of some groups of predators on the abundance of earthworms are reported.

In the beechwood studied there are a variety of arthropod (SCHAEFER, 1983a; MARTIUS, 1986; POSER, 1988) and vertebrate (CORSMANN, 1989; SAYER, 1989) species that potentially prey upon earthworms. Two experiments were devised to reveal the impact of the dominant predators of earthworms in the system under study:

(1) A fencing-out of 'macro-predators', i.e. vertebrates (especially shrews) and carabids. These groups were studied in combination because (i) the more predators are investigated simultaneously the stronger the effect to be expected, and the stronger the effect the better the chance to detect it by experimental manipulation; (ii) other predator species could not easily be handled in a fencing experiment without disturbing the structure of the habitat.

(2) A controlled microcosm study of predation by chilopods. Under field conditions of habitat structure and climate a dominant chilopod species [*Strigamia acuminata* (LEACH), known to feed on earthworms] was used as predator and lumbricids of various species were used as potential prey.

## 2. Study area

The study site is situated about 7 km east of Göttingen on the plateau of the 'Göttinger Wald', which is a submontane beechwood on limestone (410–420 m a.s.l., 10° 2′ E 51° 31′ N).

The vegetation is a *Melico-Fagetum*, subassociation of *Lathyrus vernus* (DIERSCHKE & SONG, 1982a, 1982b). Dominant herbs are *Galium odoratum* (L.) SCOP., *Mercurialis perennis* L. and *Allium ursinum* L. There is no bush layer. Besides beech, there are single trees of ash, maple and oak. The soil is a conglomerate of rendzina, brown earth and terra fusca (according to German soil classification, *cf.* SCHEFFER & SCHACHTSCHABEL, 1984).

Long-term means of temperature and precipitation at Göttingen are 8.7°C and 613 mm, respectively. Unusual climatic conditions during the experiments were a relatively warm and dry summer and a dry autumn in 1983 (annual means: 9.6°C, 588 mm).

The earthworm community is composed of the following species: *Lumbricus terrestris* L., *L. castaneus* (SAVIGNY), *L. rubellus* (HOFFMEISTER), *Dendrodrilus rubidus* (SAVIGNY), *Dendrobaena octaedra* (SAVIGNY), *D. pygmaea* (SAVIGNY), *Eiseniella tetraedra* (SAVIGNY), *Aporrectodea caliginosa* (SAVIGNY), *A. rosea* (SAVIGNY), *Octolasion lacteum* (ÖRLEY) and *O. cyaneum* (SAVIGNY). *L. terrestris* is dominant in terms of biomass, *A. caliginosa* is numerically dominant and *L. castaneus* is the dominant epigeic (for details *cf.* JUDAS *et al.*, 1989). Not all species have been found or used during the studies described here.

## 3. Exclusion of macro-predators

### 3.1. Methods

At an experimental site vertebrate predators (birds, shrews and rodents) and carabid beetles were to be excluded in order to assess the impact of these large predators on earthworm populations compared to a control plot. Vertebrates could be fenced out whereas carabids had to be removed by pitfall traps. As small-scale variations in earthworm population density can override treatment impacts, it was necessary to evaluate earthworm abundance before the start of the experiment. Hence the borders of control and experimental plots were sampled first so as to detect initial density gradients without disturbing the plots themselves.

The plots were established on 1st and 2nd October 1983, final sampling was on 18th and 19th May 1984; i.e. the exclusion was effective for 227 days.

Two adjacent 4 $m^2$ plots were chosen for exclosure and control (fig. 1). They were situated at a site with sufficient distance to trees to avoid interference with large roots. The two plots were separated by a 25 cm strip that was used for initial sampling (*cf.* below). The experimental plot was fenced with 66 cm high polyethylene plates that were tightly connected at the edges. The plates were buried to a depth of 33 cm. In order to include the factor of underground fencing of earthworm populations, at the control plot a frame of 33 cm high plates was buried to the same depth of 33 cm, and the frame's upper edges were adjusted to the soil surface in order to allow a free movement of carabids and small mammals. The exclosure was covered by coarse wire mesh to keep birds off. Leaves, twigs and snow accumulating on the wire mesh were transferred into the exclosure manually at least once per week.

At either plot eight pitfall traps were buried situated in the corners and as a central square (fig. 2). The traps were glass jars 11 cm high and 5.5 cm in diameter with a rough plastic edge attached. Plastic roofs on wire supports kept rain and snow off. The traps were frequently controlled for about two months (*cf.* fig. 4). Carabids caught at the control plot were released on the plot, those caught in the exclosure were removed from the site. The traps were closed for the rest of experimental time except for the last month in the exclosure and a short activity check in the control plot.

At the beginning and at the end of the experiment samples were taken with a square 25 cm metal sampling frame (0.0625 $m^2$) to a depth of 15 and 20 cm respectively. The ditches produced by the initial sampling of borders and central strip were dug to a depth of 33 cm, and this $-15$ to $-33$ cm soil was handsorted for earthworms in the field. In the final sampling a 0.5% formalin expulsion ($3 \times 1$ l at 10 min intervals) was applied to the holes produced by sampling. This extraction was not used in the initial sampling so as to avoid any unwanted effects of formaldehyde residues (e.g. repelling shrews) in the course of the experiment. A sampling to the depth of 33 cm is supposed to meet the aim to detect a possible density gradient prior to the experiment.

Samples were divided into the litter layer and three soil layers. Earthworms in the litter fraction were extracted by washing-sieving in water-filled whirling vessels (Judas, 1988) one or two days after sampling.

The soil fractions were stored in plastic buckets and submerged in a 10% formaldehyde solution at the end of a day's sampling. Thus, the time lapse between sampling in the field and fixation of earthworms was 14 h at the most. The extraction of animals from these preserved soil samples was conducted up to four months after sampling. It is described in the next section.

### 3.2. Extraction of soil samples by washing-sieving

#### *3.2.1. General*

The low diameter of most inorganic soil constituents allows a sieving separation of animals contained in soil samples. A mechanical extraction procedure promises better reliability than extraction procedures based on behavioural responses (heat extraction, expulsion with diluted formalin). Earthworms are rather fragile, hence an initial hardening formaldehyde fixation is necessary to avoid damage during extraction. This fixation has the additional advantage that the delay between sampling and extraction has no effect on the precision of results as compared to hand-sorting for living animals. So, many samples can be taken simultaneously and may be extracted successively without an influence of hatching or dying individuals.

This extraction of formaldehyde-preserved earthworms from soil samples is a modification of the procedure described by Bouché & Beugnot (1972). It is an adaptation to insufficient logistical capabilities and more laborious than the original device. Yet it has the advantage of being easy to install and operate. Due to the high air concentration of formaldehyde it was necessary to use a gas-mask during all stages of extraction.

#### *3.2.2. Washing-sieving*

The washing-sieving apparatus and the accessories used during the extraction procedure are shown in fig. 3.

A former top-loading washing machine was used as the washing apparatus (no. 5). The important features are the large stationary outer vessel (with effluent hose, no. 5.1) and the smaller turnable inner vessel. The latter was moved by a motor at about 4 rpm (no. 5.2).

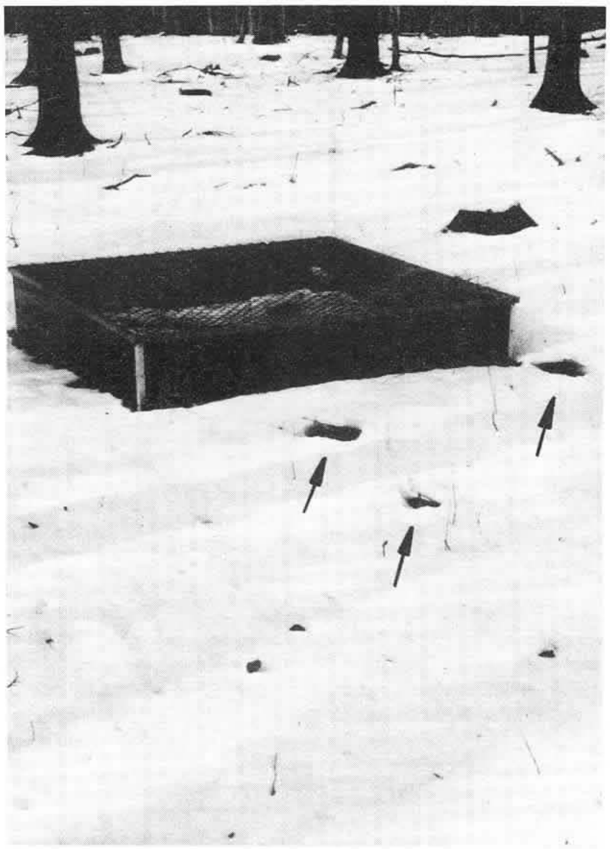

Fig. 1. Predator exclusion: the experiment *in situ*. Experimental plot in a beechwood on limestone in winter looking NW. The control plot is covered by snow, only the roofs of 3 pitfall traps are visible (arrows).

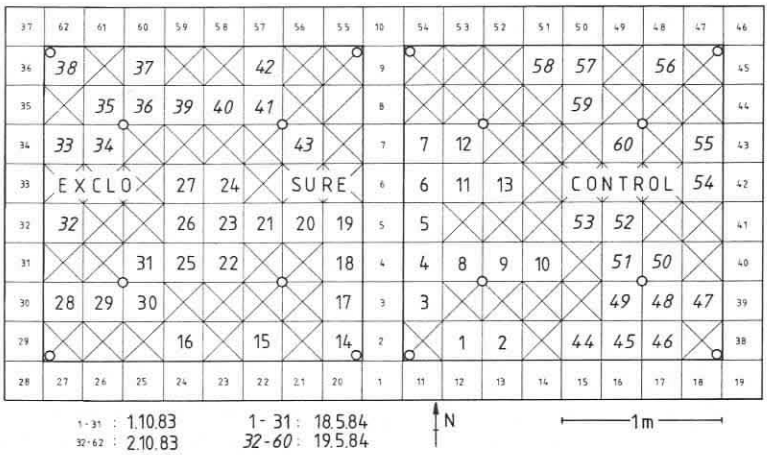

Fig. 2. Predator exclusion: Experimental design. Left: exclosure, right: control. Samples on border and central strips were taken at the beginning, samples on the plots at the end of the experiment. Circles: pitfall traps. Numbers indicate sequence of sampling. Crossed: unsampled soil. Either sampling took 2 d.

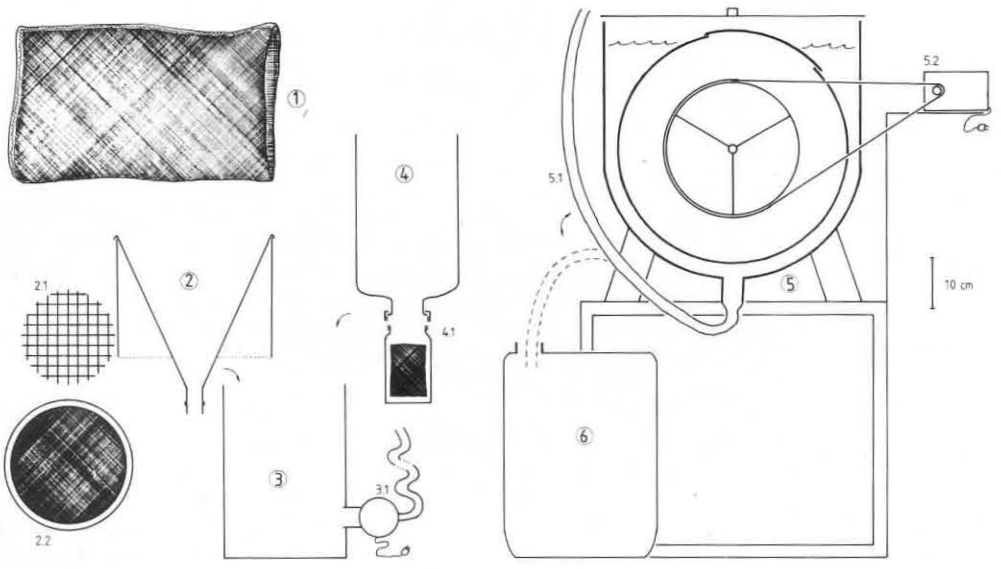

Fig. 3. Predator exclusion: Washing-sieving extraction of soil samples. Washing mashine and accessories for the extraction of formalin-fixed earthworms from soil: (1) 0.5 mm mesh nylon bag for soil samples. (2) Funnel with support to fill soil into bags, with coarse 17 mm mesh sieve (2.1). (3) Container for water circulation, with pump and hose (3.1). (4) funnel with screw-attachable 0.5 mm mesh sided collecting can (4.1) to receive washing residues. (2.2) 0.5 mm mesh sieve for funnel (2) to spread and search washing residues. (5) Washing mashine on support; the outer container has an effluent hose (5.1); the inner vessel is rotated by a motor (5.2) via driving belt and external turning wheel at 4 rpm. (6) Container for waste water.

By the water jet of a circuit pump (nos. 3 & 3.1) the soil samples were filled into 0.5 mm mesh nylon gauze bags (no. 1) attached to a funnel (no. 2). A coarse sieve (no. 2.1) in the funnel helped to remove large particles like roots, stones and leaves. The bags were closed by nylon strings and up to 12 bags were transferred to the washing vessel. Three or four washing-sieving courses were necessary:

(1) a first course (2–8 h),
(2) the main course (12–24 h) when 20–30 g of a commercial dispersion agent (main component: Na-Hexametaphosphate) was added per bag,
(3) one or two clearing courses (2–8 h).

Between the single courses the soil suspension from the washing machine was emptied into containers (no. 6) used for the safe disposal of the polluted water. Either fresh water or the cleared upper phase from these vessels was refilled.

The residues in the bags were washed with the circuit pump (nos. 3 & 3.1) through a second funnel (no. 4) into an attachable screwed receptacle with 0.5 mm mesh sides (no. 4.1). At the end they were washed onto a large fine-meshed sieve (no. 2.2) and searched for earthworms and cocoons.

### *3.2.3. Efficiency*

The efficiency of the extraction method was tested by introducing earthworms of different size classes into worm-free soil and processing these samples in the way described above.

Three test samples of 4 l of thoroughly dried soil (rendzina, brown earth and clay, respectively) from the study site were wetted with 2 l of water each. 31 earthworms of different species (*Aporrectodea* spp., *Octolasion* spp., *L. castaneus, D. rubidus*) were added to the samples, stored for 2 h, then submerged in formaldehyde, and extracted 2 d later. As small animals are most critical with regard to extraction efficiency, 18 earthworms were at most 2 cm long and 1 mm in diameter. All 31 earthworms were recovered, hence the extraction efficiency may be regarded as 100%. Two animals had injuries caused by the extraction procedure.

For future applications of the technique it has to be strongly recommended to care for good aeration of the extraction room and a constant throughflux of water if a safe disposal of polluted waste water can be guaranteed.

## 3.3. Results

### *3.3.1. Initial sampling and pitfall trapping*

The results of sampling the borders of control and experimental plots at the beginning of the experiment are given in table 1. In order to check for an underlying gradient of earthworm density, numbers are given for the centre and 6 border strips, respectively. There is no detectable gradient between the 2 plots, and differences would be insignificant if samples were taken randomly for all species but *A. rosea* (higher population density on the west/southwest border of the exclosure; a test between absolute entities [strips] is inappropriate but was used to assess the importance of absolute numeric differences with regard to a possible density gradient). Hence, a higher abundance of *A. rosea* in the exclosure **after** the experimental treatment would have been a consequence of different population densities **before** the start. All other species can be regarded as randomly distributed on the study site.

As a further assessment of inter-site differences the percentage differences of the outer borders of exclosure and control are given, respectively (table 1). The differences for all earthworms combined, *L. castaneus* and *A. caliginosa* are negligible. Besides the striking difference in *A. rosea* distribution (*cf.* above), more individuals of *Octolasion* spp. and *L. terrestris* were on the borders of the control plot. More important (in absolute numbers), there were 74 more cocoons per $m^2$ at the edge of the exclosure. This difference must be taken into account in the comparison of experimental results, as individuals hatching from cocoons are the source of population growth.

Two specimens of *Carabus nemoralis* MÜLLER, 3 *Pterostichus metallicus* (FABRICIUS) and 1 specimen of *Abax parallelepipedus* (PILLER *et* MITTERPACHER) were removed from the exclosure during the first weeks; during the last month 17 carabids were caught in the exclosure (fig. 4). Concerning the longer carabid activity at the control site in October/November, the removal of 6 carabids per 4 $m^2$ in the exclosure can be regarded as an effective reduction of carabid density at the beginning, and the 17 individuals removed in May can be regarded as newly hatched.

Rodents were active on the control plot as revealed by feces repeatedly found in pitfall traps.

### *3.3.2. Results: earthworm abundance, population structure and vertical distribution*

Table 2 gives the results of final sampling of exclosure and control plots, respectively. The total abundance in the exclosure is 9 % higher than on the control plot. Also, there is a preponderance of higher numbers for single species (0.4–38 %) and for most developmental stages in the exclosure samples, yet the differences are not significant. A surplus of 49 earthworms in the exclosure samples is balanced by lower numbers of 38 cocoons (i.e. potential individuals). More adult specimens of *A. rosea* are on the control plot, but this difference is balanced by the difference in immatures.

Comparing initial (table 1) and final abundances (table 2), overall density has about doubled. This differs between the species: *A. caliginosa* and *A. rosea* did not change in abundance. *L. castaneus, Octolasion* spp. and *L. terrestris* increased by factors of ca. 6, 3 and 2, respectively. Cocoon numbers changed to about 1/2. The increase in abundance is due to earthworms hatching during the experimental time, as absolute numbers fit rather well: lumbricids increased by 137–163 ind. $m^{-2}$, cocoons decreased by 133–154 $m^{-2}$.

Compared to control numbers, more cocoons were on the exclosure borders in the beginning (*cf.* above) and less were in the exclosure at the end, hence the higher final numbers of earthworms on the exclosure plot must be attributed to hatching during the experiment.

Predation may – without having an absolute numerical impact – change the ratio of size classes. Fig. 6 gives the developmental stages 'adult', 'immature' and 'juvenile' (defined as newly hatched by length and mass criteria) for all species found. There is no detectable difference of age distributions between exclosure and control.

Predation may not only result in numeric differences of prey species on plots with different predation intensities but may also have an influence on behavioural responses, e.g. the depth distribution of earthworms released from predation at the soil surface may shift to the litter or upper

Table 1. Predator exclusion: initial distribution of earthworms (Oct. 1983).

| species<br>N(ad:imm:juv) | all samples | | border strips | | | | | | | exclosure border | control border | diff. [%] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | W | SW | NW | Ce | NE | SE | E | W+SW+NW | E+SE+NE | |
| | n = 62 | | n = 9 | 9 | 9 | 8 | 9 | 9 | 9 | 27 | 27 | |
| | [N/m$^2$] | [N] | [N] | [N] | [N] | [N] | [N] | [N] | [N] | [N] | [N] | |
| all *Lumbricidae*<br>(below −15 cm) | 141 | 547<br>(44) | 78<br>(10) | 94<br>(1) | 69<br>(5) | 70<br>(5) | 73<br>(9) | 85<br>(6) | 78<br>(8) | 241 | 236 | +2 |
| cocoons | 254 | 983 | 182 | 202 | 110 | 120 | 114 | 144 | 111 | 494 | 369 | +34 |
| *L. terrestris*<br>23:55:2 | 21 | 80 | 10 | 6 | 13 | 10 | 12 | 16 | 13 | 29 | 41 | −29 |
| *L. castaneus*<br>0:20:4 | 6 | 24 | 2 | 4 | 5 | 3 | 2 | 5 | 3 | 11 | 10 | |
| *A. caliginosa*<br>12:68:2 | 21* | 82 | 15 | 10 | 11 | 8 | 8 | 14 | 16 | 36 | 38 | |
| *A. rosea*<br>11:119:17 | 38*** | 147 | 27[1]) | 44[2]) | 14 | 17 | 19 | 15 | 11 | 85 | 45 | +89 |
| *Octolasion* spp.<br>29:95:81 | 53 | 205 | 23 | 27 | 24 | 31 | 32 | 33 | 35 | 74 | 101 | −27 |

Nos. of border strips arranged according to geographical location (cf. fig. 2): W = 28−36; SW = 1, 29−37; NW = 37, 55−62; Ce = 2−9; NE = 10, 47−54; SE = 11−19; E = 38−46. */*** significant aggregation, P ≤ 0.05/0.001 (Chi$^2$-test). [1]) W > E (U-test, P ≤ 0.05); [2]) SW > W, NW, Ce, NE, SE, E (U-test, P ≤ 0.05). Tests according to Sachs, 1978. Numbers of ad(ult), imm(ature) and juv(enile = newly hatched) individuals per species are given. *Octolasion* spp.: *O. lacteum* and *O. cyaneum*. Diff.: [N (exclosure) − N (control)]/N (control); no difference [%] is given in case of diff. ≤ 2 individuals.

Table 2. Predator exclusion: final distribution of earthworms (May 1984).

| species | exclosure (n = 30) | | | control (n = 30) | | | diff. [%] | |
|---|---|---|---|---|---|---|---|---|
| | ΣN [ad:imm:juv] | N/m$^2$ | median N [95%] | ΣN [ad:imm:juv] | N/m$^2$ | median N [95%] | | |
| all *Lumbricidae* | 570*** | 304 | | 521*** | 278 | | + 9 | ns |
| cocoons | 188 | 100 | | 226 | 121 | | −17 | ns |
| *L. terrestris* | 79 (*)<br>22:56:1 | 42 | 2.5<br>2−3 | 71<br>14:56:1 | 38 | 2<br>2−3 | +11 | ns |
| *L. castaneus* | 82***<br>11:2:69 | 43 | 2<br>1−3 | 65***<br>7:3:55 | 35 | 2<br>1−3 | +26 | ns |
| *A. caliginosa* | 47<br>22:21:4 | 26 | 1.5<br>1−2 | 34<br>16:14:4 | 18 | 1<br>0−1 | +38 | ns |
| *A. rosea* | 83***<br>8:52:23 | 45 | 2<br>1−4 | 73<br>16:38:19 | 38 | 2<br>1−3 | +14 | ns[1]) |
| *Octolasion* spp. | 278***<br>20:50:208 | 147 | 8<br>7−10 | 277***<br>13:71:193 | 148 | 7<br>5−11 | 0 | |

*** significant aggregation (P ≤ 0.001), (*) significant regular dispersion (P ≤ 0.05, Chi$^2$-test). Numbers of ad(ult), imm(ature) and juv(enile = newly hatched) individuals/per species are given. *Octolasion* spp.: *O. lacteum* and *O. cyaneum*. Medians per sample (0.0625 m$^2$) are given with 95% confidence intervals. Diff.: [N (exclosure) − N (control)]/N (control). ns: difference between exclosure and control not significant (P > 0.05, U-test); [1]) adult *A. rosea*: control > exclosure (P ≤ 0.05). Tests according to Sachs, 1978.

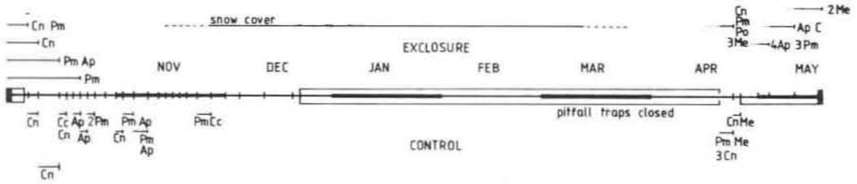

Fig. 4. Predator exclusion: Time course and pitfall catches. Horizontal line: time axis of experiment, 1st October 1983 to 19th May 1984: vertical marks: initial and final sampling (thick), control of pitfall traps (thin); boxes: pitfall traps closed. Snow cover indicated by upper vertical line; dotted: incomplete cover. Pitfall catches for exclosure and control are given above and below the time axis, respectively; marks for exclosure: time individual carabids were present; marks for control: maximum time individual carabids were not active. Ap = *Abax parallelepipedus* (PILLER et MITTERPACHER), C = *Cychrus caraboides* (L.), Cc = *Carabus coriaceus* L., Cn = *C. nemoralis* MÜLLER, Me = *Molops elatus* (FABRICIUS), Pm = *Pterostichus metallicus* (FABRICIUS), Po = *P. oblongopunctatus* (FABRICIUS).

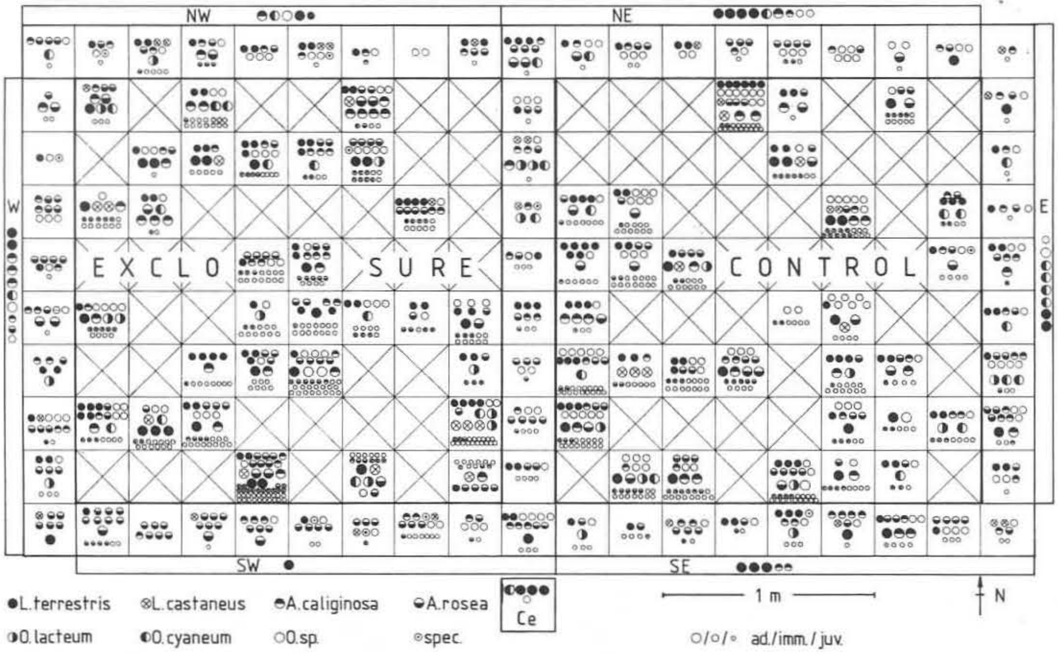

Fig. 5. Predator exclusion: Earthworm sampling. Results of initial sampling in October (border and central strips) and final sampling in May (left box: exclosure, right box: control). For each 25 cm × 25 cm sample all earthworm individuals are shown according to species and developmental stage (size of symbols: large = adult, medium = immature, small = juvenile = newly hatched). Symbols in rectangular boxes are results of hand-sorting the 6 border strips and the central strip −15 to −33 cm below the samples shown individually.

soil layers. The vertical distribution of earthworm species is given in fig. 7 for both October and May sampling. There is some difference in depth distribution between sampling dates (especially for *Aporrectodea* spp.), but exclosure and control sites have equivalent distributions by the end of the experiment.

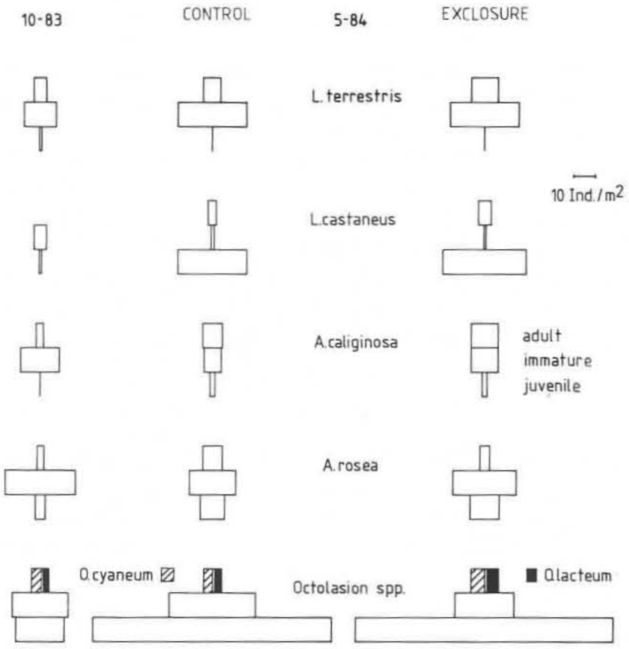

Fig. 6. Predator exclusion: Population structure of earthworm species. Left column: initial sampling (Oct. 1983), central and right columns: control and exclosure, respectively (May 1984). Numbers of developmental stages "adult", "immature" and "juvenile" (= newly hatched) are given per species.

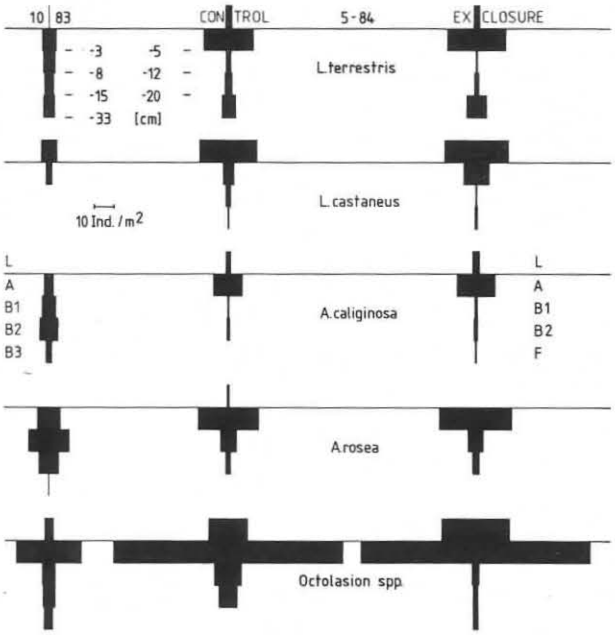

Fig. 7. Predator exclusion: Vertical distribution of earthworm species. Left column: initial sampling (Oct. 1983), central and right columns: control and exclosure, respectively (May 1984). L: litter fraction; A, B1, B2, B3: soil layers (note different depths in October and May!); F: formalin extraction (May only).

### 3.4. Discussion

Carabid population densities were $1-3\ m^{-2}$ in a nearby study in 1981 (Martius, 1986), i.e. a removal of $1.5$ carabids $m^{-2}$ in the exclosure can be regarded as an effective reduction of carabid predation in the first months of the experiment. The 17 (newly hatched) individuals per 4 $m^2$ removed in May are a major part of carabid density. Yet they have been excluded for only part of their activity period (dotted beginning of capture marks in fig. 4) and may have had some predatory impact on earthworms before being removed. That is to say, carabid predation was reduced efficiently for only part of the experimental period.

Shrews have to be regarded as the major vertebrate predators of earthworms in the study area. Unfortunately, their activity could not be studied and must be regarded as a black box system: rodents were active on the control plot (*cf.* above), since shrews are regarded as foraging there, too.

To summarize the experimental results on abundance, population structure and vertical distribution: excluding macro-predators had an impact less than the noise of small-scale spatial variation, at least in the case of the two plots studied. As the experiment was not replicated it rather gives information on two adjacent plots in a forest but on the importance of predation and release from predation. However, the results emphasize that possible effects of macro-predators are small and may be detected only by sampling with a high accuracy of estimates.

## 4. Controlled predator-prey system: chilopods and earthworms

### 4.1. Methods

In order to establish chilopod-earthworm predator-prey systems under semi-natural conditions, earthworms of potential prey size were exposed to chilopods under abiotic field conditions in microcosms with undisturbed soil structure but, yet without other animals.

Fifteen cm deep soil cores from the study site were filled into fitted cages, deep frozen to kill animals present (48 h, −20°C) and replaced into the holes. The cages were cylinder-shaped (∅ 22 cm, 30 cm high) coarse metal wire frames covered with 0.1 mm nylon mesh gauze at the sides and the bottom. The top was covered with a cotton cloth in order to allow the penetration of rainfall. As the year of the experiment was relatively dry, some water was repeatedly added in order to avoid high mortality due to drought. Time of exposure was from 5th July until 29th August 1983.

At the beginning of the experiment 10 earthworms of different species sampled near the study site were introduced into each of 5 experimental and 5 control cages (table 3, one cage received only 9 earthworms). One day later 3 individuals of the chilopod species *Strigamia acuminata* were added to each experimental cage. Animals surviving after 56 d were recovered by hand-sorting.

### 4.2. Results

The mortality rates of earthworms are given in table 4 expressed as N(not recovered)/N (introduced). In the control cages there was an overall 'natural' mortality of 31 %, ranging from 0 % (endogeic *A. caliginosa*) to 60 % (epigeics *L. castaneus* and *E. tetraedra*). In the presence of 3 specimens of *Strigamia acuminata* per cage, average mortality increased by 33 %. No difference in mortality was observed for *L. castaneus* and *E. tetraedra* (who suffered the highest control mortality). Significant differences were obtained for *A. caliginosa* (0−70 %), *Octolasion* sp. (20−53 %) and *D. rubidus* (33−70 %).

On the average, under the experimental conditions natural (drought) mortality equalled the additional predator induced mortality.

Table 3. Controlled predator-prey system: Size classes of earthworms introduced into cages with chilopods.

| size class: | | I | II | III | IV | V |
|---|---|---|---|---|---|---|
| fresh mass [mg]: | | ≤5 | 5−10 | 10−20 | 20−40 | 40−80 |
| length [cm]: | | 1−2 | 1−2 | 1−2.5 | 1.5−3 | 2−4.5 |
| diameter [mm]: | | 0.5−1 | 0.5−1 | 0.5−1 | 0.5−1 | 1−2 |
| earthworm numbers in treatment with/without chilopods | | | | | | |
| *A. caliginosa* | (N = 20) | – | 2/ | 5/1 | 2/9 | 1/ |
| *Octolasion* sp. | (N = 30) | 4/ | 4/4 | 7/9 | /2 | |
| *L. castaneus* | (N = 10) | 3/2 | 2/2 | /1 | | |
| *D. rubidus* | (N = 19) | 2/1 | 4/3 | 1/2 | 3/3 | |
| *E. tetraedra* | (N = 20) | | 5/7 | 3/3 | 2/ | |
| | ($\Sigma$ = 99) | 9/3 | 17/16 | 16/16 | 7/14 | 1/ |

Table 4. Controlled predator-prey system: Earthworm mortality in cages with/without *Strigamia acuminata*.

| | N (not recovered)/N (introduced) | | |
|---|---|---|---|
| | with chilopods | without chilopods | |
| *A. caliginosa* | 7/10 | 0/10 | ** |
| *Octolasion* sp. | 8/15 | 3/15 | * |
| *L. castaneus* | 4/5 | 3/5 | |
| *D. rubidus* | 7/10 | 3/9 | * |
| *E. tetraedra* | 6/10 | 6/10 | |
| | 32/50 = 64 % | 15/49 = 31 % | * |

Numbers given are sums of 5 replicates per treatment. Into each cage 9−10 earthworms of different species (1−3 of each species) were introduced. In the treatment "with chilopods" also 3 *Strigamia acuminata* of about 17 mg and 3 cm in length were introduced. */**: significant difference ($P \leq 0.05/0.01$, one-sided U-test [SACHS, 1978] between mortality rates of 5 replicates per treatment). Cages were exposed for 56 d from 5th July through 29th August 1983.

### 4.3. Discussion

The experimental abundance of *S. acuminata* was 84 $m^{-2}$, average natural abundance was 30 $m^{-2}$ (POSER, 1989). When spatial heterogeneity is accounted for, the experimental numbers resemble the natural ones. Also, *S. acuminata* and 7 ecologically similar *Lithobius* spp. together average 185 $m^{-2}$ (POSER, 1989), i.e. the predator density of 84 $m^{-2}$ was not unnaturally high. A mean of 280 earthworms per $m^2$ is in the order of magnitude of natural densities. However, in the field juveniles reached only half of this abundance at most (*cf.* JUDAS *et al.*, 1989). The question remains unsolved, if chilopods prey upon small earthworms at lower population densities as much as in this experiment, or if they exhibit prey switching and release earthworms from the strong predator pressure.

Individual earthworms were used randomly for treatments and replicates. Unfortunately, small size classes are predominant in the treatment with chilopods (table 3: *A. caliginosa, Octolasion* sp., all earthworms). If a higher mortality is assumed for smaller individuals, the difference between treatments could be a problem of experimental design. The following points are in favour of predation as the cause of increased mortality:

(1) The epigeic *D. rubidus* is equally distributed between treatments but shows a significant difference in mortality.

(2) The survival of individual earthworms could not be assessed throughout, yet the results for single cages do not point consistently to large individuals surviving and small ones dying.

(3) Disregarding interspecific differences, the preponderance of 7 earthworms of size classes I and II (table 3) is outweighed by the difference in mortality of 17 individuals (table 4).

## 5. General discussion

### 5.1. Predation on earthworms: other studies

The predator-prey relationship of earthworms and their vertebrate and invertebrate enemies has frequently been investigated from the point of view of the predators (for reviews see MACDONALD, 1983; LEE, 1985; GRANVAL & ALIAGA, 1988).

Some authors calculated the impact of vertebrate predators on earthworm populations:

(i) CUENDET (1983) studied in Switzerland black-headed gulls foraging in cultivated fields on earthworms brought to the surface by cultivation methods in autumn/winter when earthworms comprised 90% (mass) of the gulls' food. He concluded that gulls removed 2.5 to 3.3% of earthworm biomass and could not reduce earthworm populations effectively.

(ii) In a similar study, TOMLIN & MILLER (1988) investigated ring-billed gulls at cultivated sites in Ontario, Canada. They determined that 11% of the earthworm population (111 $m^{-2}$, 35 g $m^{-2}$) was exposed to the surface by ploughing and was thus accessible to gulls foraging immediately behind the plough. Comparing the reproductive potential of earthworms, food requirements of gulls and the short period of exposure by ploughing, they concluded that ring-billed gulls could not have a remarkable impact on earthworm populations.

(iii) KRUUK (1978) compared earthworm populations and the food intake of badgers in a habitat mixture of old and young deciduous wood, pastures and arable land. Badgers mainly fed on *L. terrestris*, and he calculated that they consumed less than 5% of average *L. terrestris* standing crop per year.

Only few studies investigated the impact on earthworm populations experimentally:

BENGTSON *et al.* (1976) studied golden plovers preying on earthworms in an Iceland hayfield *(A. caliginosa* and *L. rubellus)* in May/June. Fencing out plovers for 22 d by nets revealed a predatory reduction of total earthworm abundance by 55% (238−107 ind. $m^{-2}$), biomass was reduced by 54% (40−19 g $m^{-2}$). The experimental results fitted calculations based on observed feeding intensity of plovers. The observed heavy predation was restricted to certain fields and certain times of year.

LEE (1985) cites MOEED (1976) to have shown predation by gulls, starlings and magpies on lumbricids in a New Zealand grassland to be as strong as in the study of BENGTSON *et al.* (1976).

Experiments by SHILLITO (1960, cited in CORBET & SOUTHERN, 1977) revealed a differential predation of common shrews on groups of invertebrates in litter samples exposed to or protected from shrew predation. Lumbricid worms were taken as '2nd order' prey only.

### 5.2. Predators in the study area: the potential impact

#### *5.2.0. General*

SCHAEFER (1986) calculated the energetic relations of trophic levels in the study area. On the average, zoophagous consumption was about 30% of phyto- and saprophagous production (table 5). This situation cannot easily be transferred to specific predator-prey systems. Hence, the groups studied as potential earthworm predators in the experiments above are discussed with regard to their respective potential impact on lumbricids. Other groups of predatory species may feed on earthworms in the study area but are not considered here: parasitoid dipterous larvae [namely *Pollenia rudis* (FABRICIUS), *cf.* HÖVEMEYER, 1985], some staphylinid adults and larvae (species spectrum in SCHAEFER, 1983b) and carabid larvae (adults studied by MARTIUS, 1986, *cf.* 5.2.3.).

#### *5.2.1. Birds*

The breeding bird density was 21 pairs per 10 ha in 1981 (CORSMANN, 1989). Six ground feeding species (wood pigeon, blackbird, song thrush, tree pipit, chaffinch and robin) comprised 51% of the breeding avifauna (i.e. 11 pairs · 10 $ha^{-1}$). All but tree pipits are reported to feed on

Table 5. Energetic relations of trophic groups in a beech forest on limestone.

| Guild | B [g dry mass/m$^2$/a] | P [kJ/m$^2$/a] | $C_{Zoo}$ [kJ/m$^2$/a] | $MR_{Ap}$ 4) [mg/m$^2$/30d] |
|---|---|---|---|---|
| Zoophagous spp. 1) | 0.7 | 50 | 175 | |
| Chilopoda 2) | 0.27 | | | |
| Carabidae 1) | 0.14 | | | |
| *A. parallelepipedus* 4) | | | | 8.5 |
| Phytophagous spp. 1) | 0.1 | 6 | 29% ($P_{Phyto+Ssapro}$) | |
| Saprophagous spp. 1) | 14 | 589 | | |
| Lumbricidae 3) | 10 | | | |
| *L. terrestris* 3) | 5.6 | | | |
| endogeics 3) | 4.0 | | | |
| epigeics 3) | 0.36 | | | 2.4% ($B_{epi}$) |

References: 1) SCHAEFER, 1986; 2) POSER, 1988; 3) JUDAS *et al.*, 1989; 4) MARTIUS, 1981, material removed by *Abax parallelepipedus* ($MR_{Ap}$, for details of calculation see text). Symbols: B = biomass, P = production, C = consumption.

earthworms (GRANVAL & ALIAGA, 1988). Earthworms are classified as a main food source for blackbirds and as regular food for song thrushes (≥50% and 10–50% frequency of occurrence, respectively, GRANVAL & ALIAGA, 1988).

Of course, densities during the major part of the study were lower and overwintering birds are prevented from feeding on the ground during times of continuous snow cover. At the study site birds are rather insignificant energetically, yet passerines and especially pigeons and owls had to be prevented from incidentally foraging in the exclosure.

### *5.2.2. Rodents and shrews*

The small mammal fauna of the study area was investigated by SAYER (1989). Important rodents are *Apodemus flavicollis* MELCHIOR (dominant with <10 to >80 ha$^{-1}$) and *Chlethrionomys glareolus* SCHREBER. The dominant insectivore is *Sorex araneus* L. although its abundance could not be assessed quantitatively. Also *Sorex minutus* L. is present.

Both *A. flavicollis* and *C. glareolus* did not accept earthworms in feeding experiments (SAYER, pers. comm.), yet they are reported to use them as occasional food (≤10% frequency of occurrence, GRANVAL & ALIAGA, 1988). *S. araneus* on the other side uses earthworms as a main food source (RUDGE, 1968), hence the following calculation of potential earthworm consumption is restricted to this species.

Densities of *S. araneus* vary from 5–8 ha$^{-1}$ in grasslands (PERNETTA, 1976) up to 49 ind. ha$^{-1}$ in British woodlands (CROWCROFT, 1957, cited in CORBET & SOUTHERN, 1977). For the purpose of this calculation, a population density of 5–20 ha$^{-1}$ in the study area is assumed and may represent a realistic range (SAYER, pers. comm.). The daily consumption of one individual is given as 4–15 g fresh mass with an average proportion of 30% lumbricids (PERNETTA, 1976a). Thus, *S. araneus* consumes between 6 and 90 g ha$^{-1}$ d$^{-1}$ fresh mass, i.e. 0.03–0.5 g m$^{-2}$ a$^{-1}$ dry mass (1 g dry mass = 6.37 g fresh mass, LAKHANI & SATCHELL, 1970; 1 a = 365 d). This in turn corresponds to 0.3–5% of average lumbricid standing crop (*cf.* table 5). If only *L. terrestris* is preyed upon, the consumption amounts to 9% of this species' biomass.

The percentage of earthworms in the food may vary considerably: RUDGE (1968) found 10–12%, PERNETTA (1976b) 0–60% depending on the time of year (highest percentages in autumn/winter!). Also, lumbricid biomass varies seasonally, and the availability of earthworms may be restricted e.g. due to aestivation. This is to say that a refined calculation of potential *S. araneus* predation on earthworms would reveal some amount of temporal variation.

### 5.2.3. *Carabids*

In the study area there are 24 carabid species (MARTIUS, 1986). At least large species prey upon earthworm as a major food source (LOREAU, 1988). Their larvae have to be considered as potential earthworm predators, too (*cf.* SCHELVIS & SIEPEL, 1988), but they are neglected both here and in the experiment above.

MARTIUS (1981) determined the consumption of *Abax parallelepipedus* individuals in the laboratory: fed on mealworm larvae they consumed 14.4 mg/Ind./d at 20°C. Corrected for temperature ($Q_{10} = 2$, $\varnothing T = 10$°C), average abundance (0.22 $m^{-2}$), percentage of food unused (C/MR = 0.77), and percentage of oligochaete food items in catches from the field (13.8 %, dissection of crops), an average *A. parallelepipedus* population fed on 8.5 mg oligochaete biomass per 30 d, i.e. this species alone could remove 2.4 % of average epigeic lumbricids' standing crop per month (table 5). This is but a rough estimation: on one hand the percentage of predation on oligochaetes is underestimated (analysis based on numbers of food items instead of biomass or volume), on the other hand the degree of predation is overestimated if carabid consumption is compared to lumbricid standing crop instead of production. Yet, with the difficulties of spatial and temporal heterogeneity in mind, the above figures give an idea of the possible order of magnitude of predatory impact: as (adult) carabid density is 5 to 15 times as high as in the calculation for *A. parallelepipedus* [MARTIUS, 1986], these predators could remove 12–36 % of epigeic lumbricids' standing crop within one month (assuming the same consumption of earthworms as in the calculation above).

### 5.2.4. *Chilopods*

Chilopods are the dominant group of invertebrate predators in the study area both in terms of abundance and biomass (SCHAEFER, 1983a; *cf.* table 5). There are 10 species with an average abundance of 280 $m^{-2}$ (POSER, 1989). Most species have been shown to prey upon juvenile earthworms (≤3 cm long) in feeding experiments (POSER, 1988), and some feed on larger size classes also (e.g. several *S. acuminata* attack one large earthworm together).

In another microcosm experiment *Lithobius mutabilis* KOCH was used together with larger earthworms than in the study described above. No differences in mortality were found between experimental and control cages (*cf.* POSER, 1988). This leads to the conclusion that chilopods are important predators of earthworms, but their impact is restricted to small size classes only.

## 5.3. Impact on earthworm populations: the field situation

The above calculations of predation on earthworms are but gross comparisons of consumption and standing crop biomass. Two contrasting deviations of real world predation from theoretical considerations are possible:

(i) Effects of predation stronger than expected. This would result if not all lumbricids are equally preferred as prey but predators use earthworm species differentially and thus have a proportionately stronger effect on the very species they catch. Differential predation on two lumbricid species has been demonstrated for golden plovers by BENGTSON *et al.* (1978). Also, carabids are active mainly at the litter surface and in the litter (LOREAU, 1987) and will tend to prey upon epigeic lumbricids.

(ii) Effects of predation weaker than expected. This could be the case if variables determining predation in specific field situations have values other than in the calculations above (e.g. density, prey taken, field/laboratory consumption). But the main source of overestimating predation is the fact that consumption was compared to standing crop and neglected production of prey. The study of LAKHANI & SATCHELL (1970) of a *L. terrestris* population may give an idea of the amount of lumbricid productivity: they estimated P/B to be 33–56 % $a^{-1}$.

Another point about the possible effects of predation is the fact that abundance and biomass are two population characteristics of prey species that are affected at the same time but to a different degree. A given requirement of a predator population in terms of biomass will result in a relatively heavy loss of individuals if small prey sizes are preferred but will have a negligible numeric effect if large size classes are preferred. This bears upon the possibility of an experimental analysis to evaluate the effects of predation: individuals are the unit of population studies and biomass is a mere function of numbers (adjusted for species and size classes); hence, predation can be separated from stochastic noise most probably if it is very strong or if it is restricted to a part of the prey spectrum with a low biomass: abundance ratio.

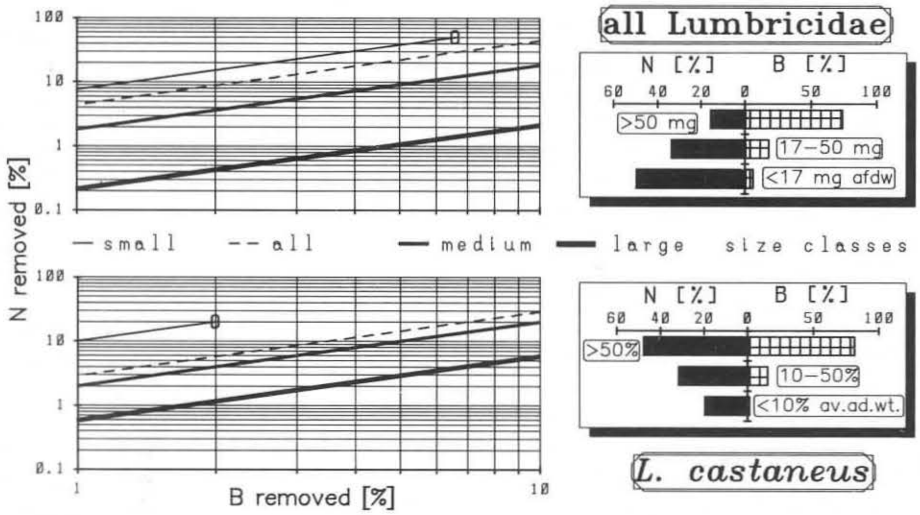

Fig. 8. Predation on earthworms: Correlates of numbers and biomass according to population structure. The percentage of individuals removed by predation as a function of percentage biomass removed is given for all earthworms (top) and *L. castaneus* (bottom), respectively. Right: proportions of numbers and biomass of 3 size classes based on one year's (1981/82) average population structure in the study area; upper figure: size classes in terms of absolute mass (maximum: 989 mg ash-free dry mass [afdm]); lower figure: size class limits as percentages of average adult mass (21 mg afdm). Left: regression lines for predation on small, medium and large size classes only and for predation on all size classes according to their numeric proportions. Endpoints of small size class regressions (o) represent the maxima of biomass and numeric percentages, i.e. no more small individuals can be removed.

In order to illustrate this argument quantitatively, the relations of numerical and biomass impact on lumbricid populations are exemplified in fig. 8 with data based on one year's average size class distribution. The calculation is given both for all lumbricid species together and for the dominant epigeic *L. castaneus*. In the case of *L. castaneus,* size classes are defined as percentages (< 10, 10–50, > 50 %) of average adult mass (21 mg dry mass). As adult mass differs between species, size classes in the case of all Lumbricidae are chosen so as to achieve a numeric pyramid of small: medium: large of about 50:30:20. If – for example – predation would remove 5 % of all lumbricids' biomass, only 1 % of individuals would be removed if earthworms of > 50 mg afdm (ash free dry mass) are preyed upon, but 40 % of numbers if individuals of < 17 mg afdm are preyed upon only. There is good reason to expect zoophagous species to differentially influence size classes of lumbricid species: LOREAU (1988) hypothesizes that carabid species differ interspecifically in prey size classes; BENGTSON *et al.* (1978) found pronounced predation on the medium of 3 size classes of 2 earthworm species.

In summary, the effects of predation can only ambiguously be deduced from theoretical calculations. Hence, the real impact of predators must be assessed experimentally. The results presented point at chilopods restricting lumbricid recruitment but "macropredators" having a minor influence on earthworm populations (although the latter point has to be taken with caution as the experiment was not replicated).

## 6. Acknowledgements

I wish to thank E. Jordan, H. H. Badstübner and the late J. Wegener for valuable help with the establishment of the soil extraction procedure. T. Poser and Dr. R. Strüve-Kusenberg contributed the larger part of conceptual and practical work in the chilopod study. I also wish to thank M. Sayer for helpful information and discussions, especially in relation small mammal predation.

## 7. References

Barnard, C. I., & D. B. A. Thompson, 1985. Gulls and plovers. The ecology and behaviour of mixed-species feeding groups. Croom Helm, London.

Bengtson, S.-A., A. Nilsson, S. Nordström & S. Rundgren, 1976. Effect of bird predation on lumbricid populations. Oikos **27**, 9–12.

– – – – 1978. Selective predation on lumbricids by golden plover *Pluvialis apricaria*. Oikos **31**, 164–168.

Bouché, M. B., & M. Beugnot, 1972. Contribution à l'approche méthodologique de l'étude des biocénoses II. L'extraction des macroéléments du sol par lavage-tamisage. Ann. Zool. – Écol. anim. **4**, 537–544.

Corbet, G. B., & H. N. Southern, 1977. The handbook of British mammals. 2nd ed., Blackwell, Oxford.

Corsmann, M., 1989. Untersuchungen zur Struktur, Siedlungsdichte und Verteilung der Brutvogelzönose eines Buchenwaldes. Göttinger Naturkdl. Schr. **1** (in press).

Crowcroft, W. P., 1957. The life of the shrew. Max Reinhardt. London.

Cuendet, G., 1983. Predation on earthworms by the Black-headed Gull (*Larus ridibundus* L.). *In:* Satchell, J. E. (ed.), Earthworm ecology – from Darwin to vermiculture. Chapman and Hall, London, pp. 415–424.

Dierschke, H., & Y. Song, 1982a. Die Vegetation der Untersuchungsfläche des SFB 135 und ihrer Umgebung im Göttinger Wald. Kurzmitt. SFB 135 **1**, 3–8.

– – 1982b. Vegetationsgliederung und kleinräumige Horizontalstruktur eines submontanen Kalkbuchenwaldes. *In:* Dierschke, H. (ed.), Struktur und Dynamik von Wäldern. Ber. Int. Symp. IVV Rinteln 1981. Cramer, Vaduz, pp. 513–539.

Granval, P., & R. Aliaga, 1988. Analyse critique des connaissances sur les prédateurs de lombriciens. Gibier Faune Sauvage **5**, 71–94.

Hövemeyer, K., 1985. Die Zweiflügler (Diptera) eines Kalkbuchenwaldes: Lebenszyklen, Raum-Zeit-Muster und Nahrungsbiologie. Ph. D. thesis, Göttingen.

Judas, M., 1988. Washing-sieving extraction of earthworms from broad-leaved litter. Pedobiologia **31**, 421–424.

– K. Poser, H.-G. Joger & M. Schaefer, 1989. Langfristige Populationsdynamik der Regenwürmer (Lumbricidae) eines Kalkbuchenwaldes. Verh. Ges. Ökol. **17** (in press).

Kruuk, H., 1978. Foraging and spatial organisation of the European badger, *Meles meles* L. Behav. Ecol. Sociobiol. **4**, 75–89.

Lakhani, K. H., & J. E. Satchell, 1970. Production by *Lumbricus terrestris* (L.). J. Anim. Ecol. **39**, 473–492.

Lee, K. E., 1985. Earthworms – their ecology and relationships with soils and land use. Academic Press, London.

Loreau, M., 1987. Vertical distribution of carabid beetles in a beech forest floor. Pedobiologia **30**, 173–178.

– 1988. Determinants of the seasonal pattern in the niche structure of a forest carabid community. Pedobiologia **31**, 75–87.

MacDonald, D. W., 1983. Predation on earthworms by terrestrial vertebrates. *In:* Satchell, J. E. (ed.), Earthworm ecology – from Darwin to vermiculture. Chapman and Hall, London, pp. 393–414.

Martius, C., 1981. Untersuchungen zur Ökologie der Laufkäfer (Coleoptera, Carabidae) eines Kalkbuchenwaldes. Diploma thesis, Göttingen (unpublished).

– 1986. Die Laufkäferfauna (Coleoptera: Carabidae) eines Kalkbuchenwaldes. Drosera **'86**, 1–11.

Moeed, A., 1976. Birds and their food resources at Christchurch International Airport, New Zealand. N. Z. J. Zool. **3**, 373–390.

Pernetta, J. C., 1976a. Bioenergetics of British shrews in grassland. Acta theriol. **21**, 481–497.

– 1976b. Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grassland. J. Anim. Ecol. **45**, 899–912.

Poser, T., 1988. Chilopoden als Räuber in einem Laubwald. Pedobiologia **31**, 261–281.

– 1989. The influence of litter manipulation on the centipedes of beech wood. *In:* Minelli, A. (ed.), Proc. 7th Congr. Myriopodology (in press).

Rudge, M. R., 1968. The food of the common shrew *Sorex araneus* L. (Insectivora: Soricidae) in Britain. J. Anim. Ecol. **37**, 565–581.

SACHS, L., 1978. Angewandte Statistik. 5th ed., Springer, Berlin.

SAYER, M., 1989. Zur Nahrungsbiologie der Kleinsäuger im Kalkbuchenwald. Verh. Ges. Ökol. **17** (in press).

SCHAEFER, M., 1982. Zur Funktion der saprophagen Bodentiere eines Kalkbuchenwaldes: ein langfristiges Untersuchungsprogramm im Göttinger Wald. Drosera **'82**, 75–84.

– 1983a. Räuberische Arthropoden in der Streuschicht eines Kalkbuchenwaldes: Biomasse, Energiebilanz, „Feinddruck“ und Aufteilung der Ressourcen. Verh. Dtsch. Zool. Ges. 1983, 206.

– 1983b. Kurzflügler (Coleoptera: Staphylinidae) als Teil des Ökosystems „Kalkbuchenwald“. Verh. Ges. Ökol. **11**, 361–372.

– 1986. Ökosystemforschung in Wäldern: Zur Funktion der Tiere. Georgia Augusta (Göttingen) **44**, 29–38.

– 1989. Die Bodentiere eines Kalkbuchenwaldes: ein Ökosystemforschungs-Projekt. Verh. Ges. Ökol. **17** (in press).

SCHEFFER, F., & P. SCHACHTSCHNABEL, 1984. Lehrbuch der Bodenkunde. 11th ed., Enke, Stuttgart.

SCHELVIS, J., & H. SIEPEL, 1988. Larval food spectra of *Pterostichus oblongopunctatus* and *Pterostichus rhaeticus* in the field (Coleoptera: Carabidae). Entomol. Gen. **13**, 61–66.

SHILLITO, J. F., 1960. The general ecology of the common shrew (*Sorex araneus* L.). Ph.D. thesis. University of Exeter.

TOMLIN, A. D., & J. J. MILLER, 1988. Impact of ring-billed gull (*Larus delawarensis* ORD.) foraging on earthworm populations of Southwestern Ontario agricultural soils. Agric. Ecosyst. Environ. **20**, 165–174.

## Addenda

(1) Sect. 5.1. (Predation on earthworms: other studies)

A second study of golden plover predation on earthworms has been carried out by BARNARD & THOMPSON (1985):

In English pastures, they compared net enclosures with control samples at the beginning and at the end of a three months' experiment from december to March. There was a 46% and a 71% drop in earthworm abundance in unprotected young and old pasture, respectively, whereas density rose in corresponding enclosures by 11 and 14%. The observed feeding rate of golden plovers amounted to about 50% of the differences between enclosed and control plots; the other 50% was attributed to predation by foxes, badgers and other birds that were also affected by the nets.

(2) Sect. 5.3. (Impact on earthworm populations: the field situation)

There is some ambiguity in the arguments about possible differences between a calculated impact of predation and an experimentally determined impact. This may be clarified by the following more formalized formulation:

The calculations of predatory impact on earthworms are based on comparisons of predator consumption (C) and prey standing crop biomass (B), and effects of predation may be (i) stronger than expected if only a fraction $B_p$ of B is relevant to predation, i.e. $C/B_p > C/B$.

(ii) weaker than expected due to prey production (P). If consumption is increased or diminished in an experiment, the expected change in B can be calculated as the imposed change in C, i.e. $\Delta B_1 = \Delta C$. But the demands of predators are at least in part met by prey production ($P_c$), and therefore prey standing crop will not change as a function of C/B but as a function of $C/(B + P)$, and $\Delta B_2 = \Delta C - P_c < \Delta B_1$.

In the long run, the relation of C to P is the interesting aspect of predation, as seasonal and local characteristics of the $C/(B + P)$ ratio will determine whether predators may have a regulating influence on their prey.

**Synopsis:** *Original scientific paper*

JUDAS, M., 1989. Predator-pressure on earthworms: field experiments in a beechwood. Pedobiologia **33**, 339–354

In a submontane subatlantic beech forest on limestone two experiments were carried out to reveal the influence of zoophagous species on earthworm populations:

(1) Macro-predators (birds, shrews, rodents, carabids) were fenced out from an experimental plot for 7,5 months (October to May). In order to achieve a high reliability of sampling so as to be able to detect small differences in abundance, a washing-sieving procedure for soil samples was developed that was 100% efficient. Population structure and vertical distribution equaled those on a control plot. Differences in abundance were not significant.

(2) Juvenile earthworms were exposed to the chilopod *Strigamia acuminata* in microcosms under field conditions for about two months. Average earthworm mortality was 64% compared to 31% in controls.

**Key words:** Predation, Lumbricidae, Chilopoda, Carabidae, Vertebrata, extraction method.

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